BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. APRIL 8, 1961 NUMBER 136

NOTES ON HISPANIOLAN HERPETOLOGY 3. THE EVOLUTION AND RELATIONSHIPS OF THE *ANOLIS SEMILINEATUS* GROUP

BY ERNEST E. WILLIAMS

The discovery of a third species of the *Anolis semilineatus* group, confined apparently to the high interior of the Dominican Republic, poses problems in the distribution, biology and evolution of the group.

The distributional data for the *semilineatus* group has been given in Williams and Rand (1961) and need not be repeated in detail here. *A. semilineatus* and *A. olssoni* are both widely distributed north of the Cul de Sac Plain but occupying ecologically somewhat different situations and thus with but limited actual contact or overlap; only *A. semilineatus* at present is known south of the Cul de Sac Plain in the southwest and Barahona peninsulas.

A. cochranae is found in the center of Hispaniola in the Cordillera Central — geographically in the midst of the other two species though its contacts with these others are not known. The biological peculiarity in the relation of *A. cochranae* to *A. semilineatus* has also been pointed out in Williams and Rand (1961). Thus, though differing strongly from the closely related *A. semilineatus* in certain scale characters, *A. cochranae* is identical in body and dewlap color. This phenomenon is highly unusual in the genus *Anolis* in which body and dewlap color differences are important cues in species recognition. (There are, for example, strong body and dewlap color differences between *A. semilineatus* and *A. olssoni*.) *A. cochranae*, if it is in contact with *A. semilineatus*, as *A. semilineatus* and *A. olssoni* are in contact with one another, would seem to be a most anomalous case in which it would be necessary to provide some *ad hoc* explanation — such as some unknown behavior difference — for the maintenance of the species distinction.

The problem is thus to provide an explanation of the central geographic position of *Anolis cochranae* in Hispaniola and of the curious absence in *cochranae* of the usual anoline species recognition characters *contra* a related species that occurs literally on every side of it.

I propose below a suggested history of the *semilineatus* group that appears to solve this problem. It must be admitted that this proposed history depends upon taking at face value the distributions of the three species as they are known at present. This is patently unsafe, but it provides a useful starting point.

On our present knowledge of distribution it is simplest to suppose that the postulated biological problem has not arisen, that *cochranae* and *semilineatus* are nowhere in contact. This is at the moment only a brave hypothesis. *Anolis cochranae* is known from only two collections; our more extensive knowledge of the distributions of *semilineatus* and *olssoni* is by no means good enough to prove contact or absence of contact with *cochranae*.

Critical to the proposed history is the supposition — uncontradicted by the available evidence — that *olssoni* is really absent from the southwest and Barahona peninsulas. It does appear to be absent from the moist coastal zone at Aux Cayes (observations by A. S. Rand and J. Lazell in 1960) and Rand did not collect it in the dry area of Oviedo on the Barahona peninsula in 1959. It is not present in Hassler's collections from these two areas.

Let us then take the present distributional evidence at face value. Let us assume then that *semilineatus* is the only grass anole of the southwest and Barahona peninsulas and that *olssoni* just touches this area at the southern edge of the Cul de Sac Plain.

The southwest and Barahona peninsulas taken together are just that portion of the island which was cut off from the mass of Hispaniola by the Pleistocene seaway through what is now the Cul de Sac Plain. Residual salt lakes and coral rocks still testify to this former seaway.

The division of Hispaniola into two parts which resulted from this seaway provides two suitable theatres — a main island and a southern counterpart — for the classic pattern of speciation during separation, and intensification of species difference ("character displacement") during renewed contact.

On this hypothesis *semilineatus* is the autochthonous grass anole of the southern cut-off portion of Hispaniola and *olssoni*

and *cochranae* autochthons of the northern main mass of the island. *Semilineatus* has infiltrated the northern island all but completely, while *olssoni* is not known to have invaded the southern island.

The spread of *semilineatus* through much of the northern island is not too surprising in view of its eurytopic ecology (Mertens, 1939, Williams and Rand, 1961). Though characteristic of a specialized open habitat, it seems to be sufficiently tolerant of forests that these would be less efficient barriers to its spread than they would to stenotopic *olssoni*. It is somewhat more surprising — if it is true — that *olssoni* has not spread along the dry north coast of the southwest peninsula or the east coast of the Barahona peninsula, but it would be stopped easily by discontinuities in suitable habitat and would for this reason be unlikely to reach localities otherwise quite suitable to it on the southern island.

The different coloration in *olssoni*, including the dewlap color, and the large size of the dewlap scales may well have developed after *olssoni* came into secondary contact with *semilineatus* during the latter's invasion of the northern island fragment. In suggesting this we assume that the features in common of *cochranae* and *semilineatus* are primitive and that modification in these features took place exclusively or almost so in *olssoni*. (Surely the lack of enlargement in the gular scales is primitive in *semilineatus* and *cochranae;* this leaves only color in question.)

What, however, about the origin and relationship of *cochranae* and *olssoni?* It must first be noticed that there is some plausibility in considering these two more closely related to each other than to *semilineatus*. In body squamation (i.e. scale size), *cochranae* and *olssoni* are very similar. This is a feature which, unlike the characters of the dewlap or of body pattern, is unlikely to be a matter of intra- or inter-species recognition. We do not know that it is *per se* adaptive: the difference in scale size between *semilineatus*, on the one side, and *cochranae-olssoni*, on the other, is more likely to be the external expression of more fundamental genetic divergencies.

No physiographic barrier, however, will account for the division of the grass anole population of the northern or main Hispaniolan island into two species. It is necessary to suppose that the barrier was an area of unsuitable ecology, i.e. moist dense forest. *Olssoni* may then be supposed to have arisen in

the arid coastal lowlands while *cochranae* arose in the open areas of the high pine woods[1] of the interior valleys of the Cordillera Central. (We note that Wetmore and Swales, 1931, p. 24, describe the natural vegetation of the Valle Constanza as "forests of open pine mingled with areas of dense rain forest.")

The known habitat of *cochranae* — Valle Constanza — is a high interior valley of the Cordillera Central. Though the floor of this valley is not very high (*ca.* 3000 feet) it is surrounded by some of the highest peaks in Hispaniola and ingress to it at moderate elevations is somewhat narrow and limited. In such an area a grass anole population might indeed enjoy a measure of isolation from other grass-bush populations — the more so if we suppose that the separation of *olssoni* and *cochranae* dates from a period in which the density of the hardwood forest of intermediate elevations was at a maximum.

Relationships of the *semilineatus* group.

There are no other anoles in Hispaniola which either very much resemble or seem very closely related to the *semilineatus* group. A search for close relatives and ancestors takes us at once outside Hispaniola.

Two Greater Antillean groups of *Anolis* are structurally similar — the *alutaceus-clivicolus-cyanopleurus-spectrum* group in Cuba and the *krugi-pulchellus-poncensis* series in Puerto Rico. (None of the anoles of Jamaica or the Bahamas are similar either ecologically or structurally.)

Both the Cuban and the Puerto Rican series share with the *semilineatus* group the middorsal zone of enlarged scales (least developed in *krugi* of Puerto Rico). All except *alutaceus-clivicolus* have keeled ventrals.

The Cuban anoles are all forest species, *A. alutaceus* occurring in rather deep shade, *A. spectrum* in less deep shade. But, though in this regard they differ from the Hispaniolan species which are fonder of open areas, they are closer to the *semilineatus* group in structure than are the Puerto Rican species. Like the *semilineatus* group they are small, usually under 40 mm snout-vent length, slender, with large dewlaps and well developed postanal scales in the males. In color, however, they differ in never possessing the flank stripe so characteristic of the *semilineatus* group, tending instead to emphasize the light middorsal stripe.

[1] Pine in Hispaniola, in contrast to e.g. Cuba, is confined to higher elevations.

Of the *alutaceus* series, *clivicolus,* which may be a subspecies of *alutaceus,* has the least slender habitus and the least specialized squamation. It is easy to envision this as representing the primitive stock of this series.

The Puerto Rican series is, on the other hand, more similar to the Hispaniolan species in habits. Two of the three species — *pulchellus* and *poncensis* — are "grass anoles" or at least anoles of open reaches. The third species — *krugi* — is an anole of denser brush. All are larger than any species of the *semilineatus* group — nearer 50 mm than 40 mm snout-vent length. They are perhaps not as slender as their parallels in Hispaniola (though this is a character difficult to estimate objectively); the dewlaps are relatively small and the postanal scales poorly developed. All three have a flank stripe passing forward through the eye more or less well expressed.

In both Cuba and Puerto Rico the series exhibit a wider range of structure than do the Hispaniolan forms. In each series there is a species with the middorsal zone of enlarged *keeled* scales less developed than in any Hispaniolan species (in Cuba — *clivicolus-alutaceus,* in Puerto Rico — *krugi*) and one with this zone much more strongly developed than in any Hispaniolan species (in Cuba — *spectrum,* in Puerto Rico — *poncensis*). One difference appears in this regard: in all the Cuban forms the width of the zone of enlarged dorsal scales is about the same (*ca.* 8 scale rows as compared with *ca.* 10 in Hispaniolan forms), while in the Puerto Rican forms concurrently with increase in the size of the middorsal scale zone, there is an increase in the number of rows enlarged (*ca.* 4 in *krugi, ca.* 12 in *pulchellus,* 15+ in *poncensis*).

The evaluation of these resemblances, which are in each case beset with significant differences, is difficult. Parallelism is very probable, and it is especially likely that the Puerto Rican series is an independent radiation within Puerto Rico from the same stock that gave rise to *A. cristatellus, A. stratulus, A. gundlachi* and *A. evermanni.* The primitive member of the Puerto Rican series, *A. krugi,* is not very different from *cristatellus* and *gundlachi* and would certainly be classed with them except for its obvious position at the base of a small grass anole radiation on Puerto Rico.

The Cuban anoles which display a strong structural affinity *in spite of some habitat difference* are more probably close relatives of the Hispaniolan series. There is in fact no substantial reason for doubting the relationship.

It must be pointed out that the squamation pattern with a strongly developed middorsal zone of enlarged keeled scales, smaller laterals, and strongly keeled ventrals as large or larger than the middorsals is common in mainland *Anolis,* particularly so in Central America. This pattern occurs also in the Greater Antilles in three species which, though certainly anoline, are currently referred to other genera: the Cuban species (*ophiolepis*) to *Norops,* and a species from Navassa (*barbouri*) along with one from Hispaniola (*wetmorei*) to *Chamaelinorops.*

The mainland forms exhibit a whole spectrum of conditions in regard to the distinctness, number of scale rows, size of scales involved in the dorsal zone, etc. No described form seems close enough to the Hispaniolan or Cuban grass anoles to be worth serious consideration as representing the ancestral stock.

Norops ophiolepis, which occupies the grass anole habitat in Cuba, does not seem related either. It has some features peculiar to itself — the reduction of the canthal ridge scales to two, the small number of scales in the loreal area (*ca.* 10-12), the very elongate scales between the nostrils, the large mental scales — that are unlike not only the *semilineatus-alutaceus* groups but its supposed congeners on the mainland. The relationships of *ophiolepis* are probably with *Anolis sagrei* and more remotely with the *homolechis* complex; there are certainly no grounds for postulating close affinity to the *semilineatus-alutaceus* set.

Chamaelinorops barbouri and *C. wetmorei* are even more distinct. The basic pattern of squamation is quite heterogeneous and yet upon this has been imposed a second pattern of enormously enlarged keeled dorsals and hugely enlarged keeled ventrals exaggerated beyond that seen in any other forms.

This picture, like the apparent radiation of forms on Puerto Rico and the extraordinarily varied array of forms on the mainland, suggests strongly that the pattern — enlarged middorsal zone, enlarged keeled ventrals — is one of several stereotypes that the anoles have again and again produced, that this is one of a limited set of squamation patterns possible to the anolines and therefore produced in parallel fashion in many times and places.

It is this parallelism that contributes to the notorious "difficulty" of the genus *Anolis.* Narrow groups are rather easy to recognize (though the specific and infraspecific structure within

the group may be puzzling in the extreme) but wider relationships (at least when externals only are considered) are problematical, becoming obscurer with each step more distant from the species group.

Origin of the *semilineatus* group

The species of the *semilineatus* group are more uniform than the related Cuban series. They most resemble *cyanopleurus*, the middle term in the morphological series of Cuban forms. This species has its range in extreme eastern Oriente and is thus geographically closest to the Hispaniolan group. It therefore seems probable that the *semilineatus* series on Hispaniola has been rather recently derived from a *cyanopleurus*-like Cuban ancestor but has been on Hispaniola long enough to achieve island-wide dispersal and moderate differentiation at the specific level.

Acknowledgments

I have had the advantage of discussions with A. Stanley Rand and with Dr. Richard Etheridge. The latter's osteological evidence for species groupings within *Anolis* (unpublished thesis, University of Michigan) has in part confirmed, in part guided my own thinking on the wider relationships of *Anolis* species.

The map-diagram was prepared by Patricia Grubbs.

REFERENCES CITED

Meetens, R.
1939. Herpetologischer Ergebnisse einer Reise nach der Insel Hispaniola, Westindien. Abhandl. Senckenberg. naturf. Ges., **449**: 1-84.

Wetmore, A. and B. H. Swales
1931. The birds of Haiti and the Dominican Republic. Bull. U.S. Nat. Mus., **155**: 1-483.

Williams, E. E. and A. S. Rand
1961. Notes on Hispaniolan Herpetology. 2. A review of the *Anolis semilineatus* group with the description of *Anolis cochranae*, new species. Breviora, No. **135**: 1-11.

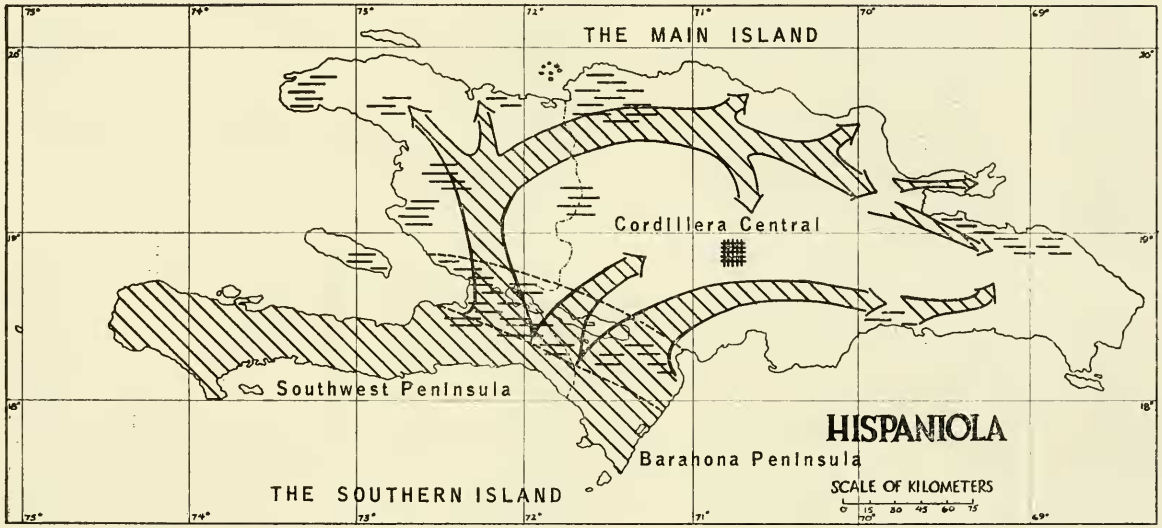

Diagram of the hypothetical invasion of the main mass of Hispaniola by *Anolis semilineatus*. The distribution of *A. semilineatus* is represented as continuous only for sake of convenience. The distributions of *A. olssoni* and *A. cochranae* are, in contrast, represented as disjunct or isolated, to correspond with present information; they may be more extensive or more nearly continuous than is indicated. See map in Williams and Rand (1961) for actual locality records for all three species.